

Thermoregulation of the Pup and Adult Weddell Seal, *Leptonychotes weddelli* (Lesson), in Antarctica.

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(Plates I-II; Text-figures 1-8)

INTRODUCTION

SOME phocid seals are the most polar of marine mammals and live in the thermally most difficult of environments for homeotherms. They are confronted with extreme problems of heat conservation in the coldest of seas and with problems of heat dissipation when hauled out on the ice to pup, molt, or rest. Their thermoregulation, therefore, illustrates some important facets of mammalian adaptation.

The Weddell seal, *Leptonychotes weddelli* (Lesson), is typically an inhabitant of the shore and fast ice of Antarctica, frequenting the most southerly open water, leads, or access holes. It probably lives at the lowest mean environmental temperature of any mammal on a year-around basis. The water of its environment is almost always close to the freezing point even in summer, when air temperatures rarely rise above 5°C. Its biology has been reviewed by Wilson (1907), Lindsey (1937), Bertram (1940), Sapin-Jaloustre (1952), Scheffer (1958), Mansfield (1958), King (1964), and Smith (1965, 1966). Recently, attention has been turned to its underwater biology, for instance, Littlepage (1963), Ray and Lavallee (1964), Kooyman

(1965), Schevill and Watkins (1965), and Ray (1965, 1966, 1967). The species is an ideal subject for field study.

Previous work on the thermoregulation of pinnipeds, such as the important studies of Irving and Hart (1957) and Hart and Irving (1959), has for the most part emphasized physiological aspects in restrained animals: the skin/ambient temperature regression, the metabolic rates, the definition of thermoneutrality, and the establishment of critical temperature limits. Fay and Ray (1968) and Ray and Fay (1968) have used a somewhat different approach in which behavioral and physiological mechanisms were considered simultaneously in wild and unrestrained captive walruses. Their remarks and methods apply here: in sum, that wild animals rarely expose themselves for prolonged periods to conditions where critical limits apply; that a "tolerance zone" in which thermoneutrality is maintained is more applicable for animals in nature; that behavior (including "escape") and physiology are mutually responsible for the delimiting of this zone; and that a study of the unrestrained animal helps to reveal the relationship between physiology and behavior.

In the present study we report on work done almost solely on unrestrained Weddell seals in the field in Antarctica in an effort to delimit the tolerance zone of the Weddell seal. In addition, some years ago it was suggested to one of us (Ray) by L. Irving (pers. comm.) that one aspect of pinniped thermoregulation had been ignored: the physiological change that the

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lanugo-clad, almost blubberless, mostly terrestrial pup undergoes to become a more thinly haired, thick-blubbered, amphibious postlanugo animal. Since that time, the work of Davydov and Makarova (1964) has appeared, in which pup harp seals, *Phoca groenlandica*, were subjected to metabolic tests. It was shown that metabolism decreases directly with the accumulation of subcutaneous fat and increases the tolerance of lower water temperatures. In the present study, we have dealt with the Weddell seal principally in air and have utilized almost identical methods for pups, juveniles, and adults on the assumption that the changes in the insulative layers from birth to weaning are responsible for no less significant changes in behavioral and physiological thermoregulation. In contrast with Davydov and Makarova, we have not utilized an experimental approach, but rather an ecological one. As in Fay and Ray's work, we have paid particular attention to adaptations for heat dissipation near the upper tolerance limits, partly owing to difficulties of observation in cold or inclement weather.

MATERIAL AND METHODS

Data were gathered almost entirely from wild and penned animals in Antarctica. Wild animals were easily accessible by tracked vehicle from McMurdo Station. Penned animals were two adult females and their pups that were netted and airlifted by helicopter to wood-slatted, 5-by-5 meter pens placed on the sea ice 0.5 kilometer west of McMurdo Station.

During the spring season when most of our work was done, Weddell seals were mostly gathered in rookeries or smaller nonbreeding groups from Scott Base, Hut Point Peninsula, to Cape Royds: i.e., between 77° 33' and 77° 52' south latitude, and 165° 5' and 166° 53' east longitude. Temperatures are not so extreme as they are in the interior of the continent, but are more so than in similar arctic latitudes, owing to higher velocity winds of colder temperatures from the south polar plateau.

Physiological measurements were made on slightly disturbed or undisturbed animals except for thermal gradients in the superficial tissues of adults, which were taken immediately after death from animals killed for other purposes (dog food, specimens). A few observations were also made for comparative purposes on captives that were returned to the New York Aquarium, but no physiological data from them are indicated on our graphs. Skin samples were taken in the field and returned to New York for tanning and study. Respiratory and heart rates were

taken visually, or, in the case of the latter, occasionally by means of a Cambridge Trans-Scribe electrocardiograph. Temperatures were taken with a six-channel Yellow Springs telethermometer; the most efficient probe proved to be a 20-gauge hypodermic type, which stabilized rapidly. A few temperatures were taken with Weston thermocouples when the telethermometer was not available. Rectal temperatures were taken on 15- to 30-cm penetration unless otherwise specified.

One pup was kept crated for a time in front of the biological laboratory for metabolic tests. When the gut was empty, the pup was sealed for one to two hours in a sheet-steel chamber, 1-by-1-by-2-meters, from which air samples were taken from two heights with 10-cc syringes through rubber stoppers in the chamber. Gas analyses were made with a Scholander 0.5-cc analyzer (Scholander, 1947).

Orientation and behavior studies were made visually from the ground and from the air. Aerial photography was used most to determine orientation to the sun.

In an effort to standardize, we made extensive tests to determine the best location on the seal's body for the taking of skin temperatures. In all cases, unless otherwise specified, temperatures are those from the dry body or flipper perpendicular to the sun, or, if in cloudy weather, farthest from the ice surface. This minimized the effects of dampness and vasoconstriction. Data from wet animals were treated separately. In a few cases, we were able to take skin temperatures from submerged or recently emerged animals to note the extent of vasoconstriction upon exposure to ice water.

For every physiological measurement, micro-environmental weather data were taken. Being cognizant that ambient shade temperature is not the only parameter of weather that affects thermoregulation, we have used "effective temperature" (cf. Eagan, 1964, & Folk, 1966), calculated here as follows: the black-bulb temperature in still air was taken in the seal's micro-environment as a measurement of insolation, and from this temperature one degree centigrade for every mile per hour of wind was subtracted. There was a slightly better alignment of data when using effective rather than ambient temperatures (Text-figs. 1-4), but the major advantage was that effective temperature gives a more realistic environmental parameter when insolation and/or wind are strong. For instance, Fay and Ray (1968) have shown that insolation and wind act independently of ambient temperature in influencing behavioral thermoregulation.

The dotted lines drawn on the graphs of Text-figs. 1-4 are our estimates of maximal skin temperatures in air. It is neither practical nor realistic to use statistical methods (i.e., regressions) in this work since "plateau" limits of temperature during vasodilation (Ray & Fay, 1968), not "average" skin temperatures, are probably more meaningful in adaptation.

RESULTS

Internal Temperatures

Only five measurements were made rectally but indications are that the internal temperature of the Weddell seal is close to 37°C. Three rectal temperatures of penned pups were all 37°C. The importance of adequate penetration into the rectum is illustrated by other two temperatures taken in adults: 5°C circumanally and 28°C upon only 7.5-cm penetration. Both of these animals were lying on ice in subfreezing air. Thermal gradients (Text-fig. 7) also indicate a core temperature at or very near 37°C, as indicated by deep blubber and muscle measurements near this temperature.

Temperature of the Skin When Wet

We had few opportunities to obtain surface temperatures on swimming, wild Weddell seals (Table I). One slightly active adult in the water

tive temperatures as high as 11°C. The highest skin temperatures were obtained upon emergence into air of the warmest effective temperature, in agreement with data obtained for walruses by Ray and Fay (1968).

Temperature of the Dry Fur and Skin

For adults, temperatures of the outer fur surface and the skin were taken from the same location on the body. For pups, the same applies, but the 2.0-2.5-cm thickness of the lanugo made possible the additional measurement of fur temperatures 1 cm beneath the surface. For both adults and pups, the skin temperatures of the flippers were taken at the flipper tip and on the membrane halfway to the tip from the ankle.

Adult fur-surface temperatures were usually not more than about 10°C higher than effective temperatures until about freezing, when the gradient was greater (Text-fig. 1). Fur temperatures rose as a straight regression with effective temperatures. Skin temperatures were considerably higher than fur temperatures. None was below freezing, but some were as low as 0 to 7°C at effective temperatures of -13 to -21°C. Skin temperatures did not rise as a straight regression with effective temperatures, but reached a plateau of about 34°C at effective temperatures over -13°C.

Pup fur-surface temperatures were similarly

TABLE I
SKIN TEMPERATURES OF WEDDELL SEALS WHEN IN WATER OR JUST EMERGED

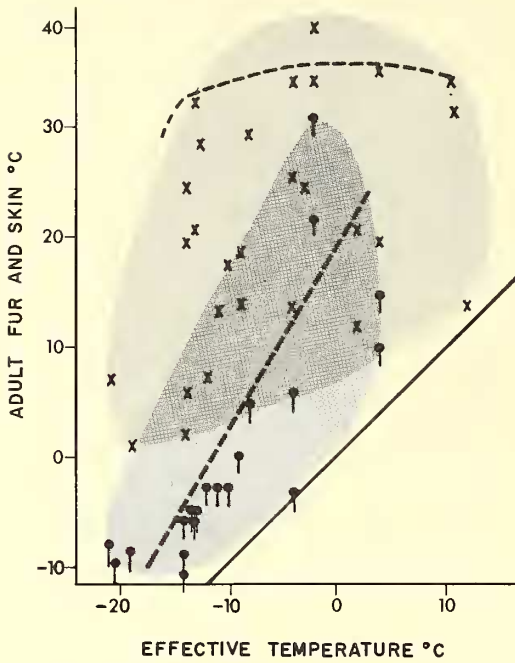
<i>Effective Air Temperature</i>	<i>Water Temperature</i>	<i>Skin Temperature</i>	<i>Flipper Temperature</i>	<i>Remarks</i>
-6.0	2.5	8.5	Adult, just emerged
....	-2.5	-2.0	Adult, in water
11.0	20.0	18.0	Adult, recently emerged
-19.0	10.0	2.0	Pup, just emerged
-19.0	-2.5	-1.0	Pup, just emerged
11.0	23.0	16.0	Pup, just emerged

of an access hole had a skin temperature a fraction higher than the supercooled -2.5°C water, confirming the data of Irving and Hart (1957). Just under the ice surface, the water temperature was -1.9°, in which case the water/skin gradient would be slightly smaller.

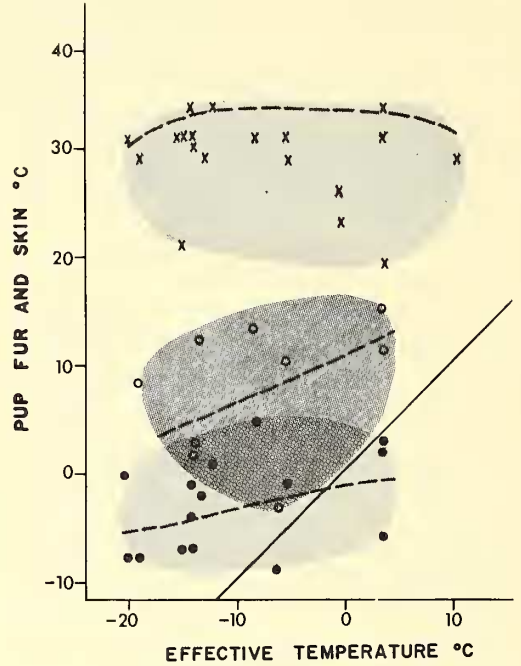
We were able to obtain data from five just-emerged animals (Table I). All animals tested had been out of water less than five minutes and most about a minute, yet skin temperatures rose in that short time to a maximum of 23°C and flipper temperatures to 18°C in air of effec-

low at low effective temperatures but did not rise as fast as those of adults (Text-fig. 2). We attribute the presence of fur-surface temperatures lower than the effective temperatures (in the upper range) to the fact that their fur was often slightly damp from melted snow. The fur temperature a centimeter below the fur surface was considerably higher than the fur-surface temperature. Skin temperatures were almost always high, plateauing at about 34°C at effective temperatures from -20 to 10°C.

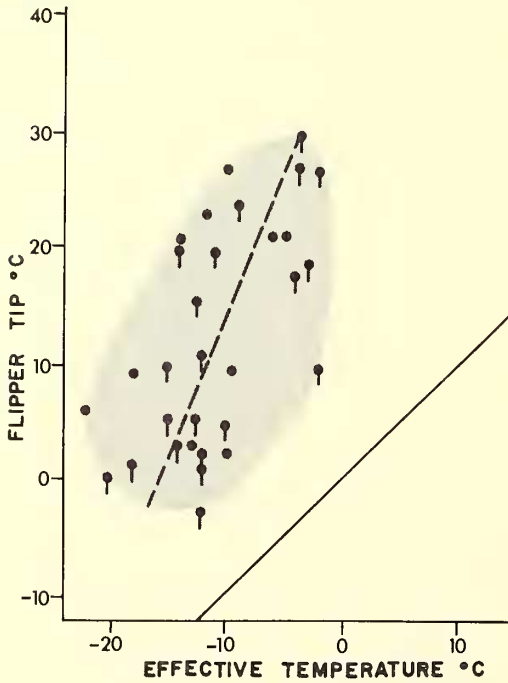
The flipper tip temperature of adults and pups



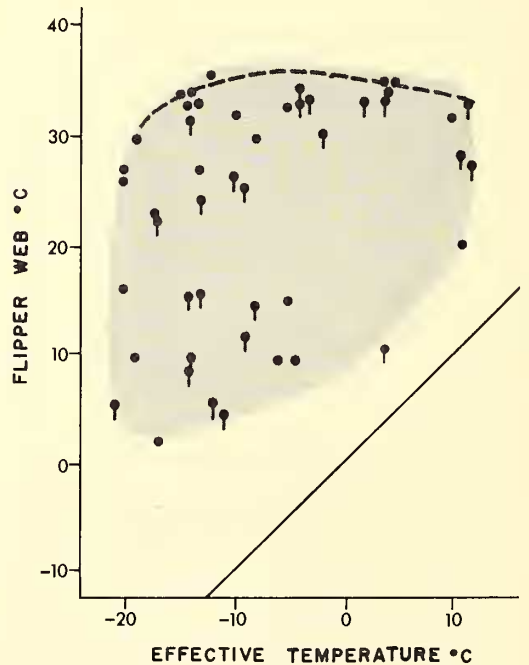
TEXT-FIG. 1. Temperatures of the dry fur surface (= ♢) and skin (= x) of adult Weddell seals at rest in air.



TEXT-FIG. 2. Temperatures of the fur surface (= ●), fur 1 cm beneath the surface (= ○) and dry skin (= x) of pup Weddell seals at rest in air.



TEXT-FIG. 3. Temperatures of the flipper tip of adult (= ♢) and pup (= ●) Weddell seals at rest in air. The flipper tip was often wet or damp.



TEXT-FIG. 4. Temperatures of the dry flipper web of adult (= ♢) and pup (= ●) Weddell seals at rest in air.

rose as straight regressions with effective temperature (Text-fig. 3). The temperature at the tip of the flipper descended to -4°C at an effective temperature of -13°C and rose to 30°C at an effective temperature near freezing. The flipper tip of both adults and pups was often damp with melted snow, urine, or excrement. The flipper membrane of adults and pups was similar to the body skin temperature, reaching plateaus of about 34°C at effective temperatures over -15°C (Text-fig. 4).

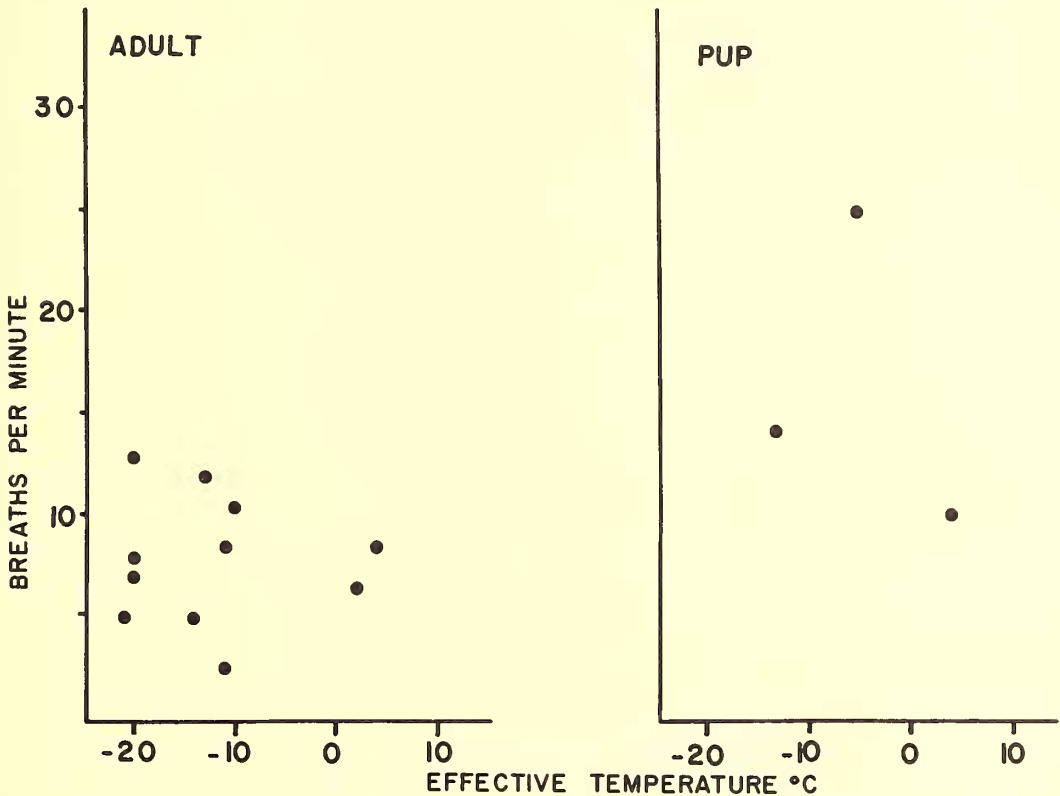
Data were also obtained for skin temperatures from the base of the flipper (ankle) and the pelvic region (hip) in an effort to establish a gradient from flipper tip to body. However, these results were indistinguishable from each other and from temperatures of the body skin and flipper web and so are not figured.

Vasoconstriction for body skin, where temperatures would not rise to plateau levels, might occur at effective temperatures below about -13°C for adults and -15°C or lower for pups. Our estimated slopes, shown by dotted lines on Text-figs. 1-4, indicate that skin temperatures

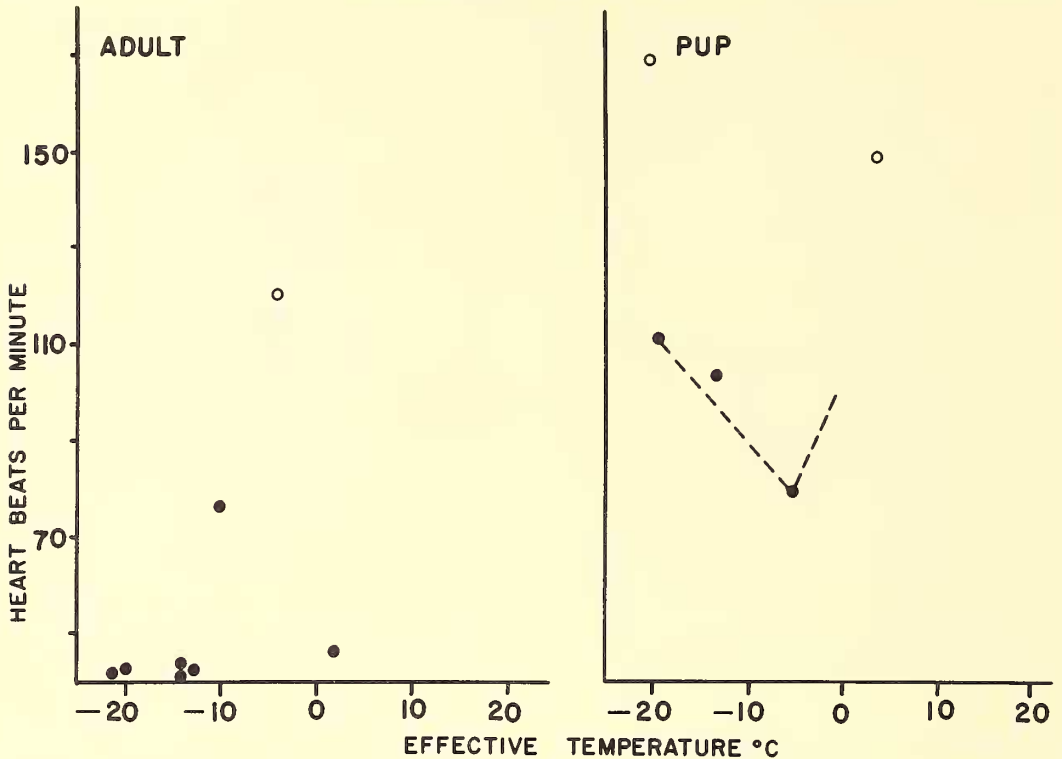
might not descend to 0°C until effective temperatures of at least -30°C are attained, but data at these low effective temperature levels are not available.

Breathing and Heart Rates

Our few data, all from resting animals, are presented in Text-figures 5 and 6. It is immediately apparent that pups had higher breathing and heart rates than adults, reflecting higher metabolic rates as well. For adults, the average heart rate was 56 per minute and the average breathing rate was 7.8 per minute. For pups, these rates were 123 and 16.3, respectively. It was noted that marked bradycardia occurred when the breath was held and that both rates were highly irregular. Heart rates taken by aid of an electrocardiograph were relatively high owing to the disturbance caused to the animal. We were unable to demonstrate a correlation of these rates with effective temperature, as for walruses in Ray and Fay (1968), though it is possible that pup heart rates were minimal at about -5°C effective temperature.



TEXT-FIG. 5. Breathing rates of adult and pup Weddell seals at rest in air.



TEXT-FIG. 6. Heart rates of adult and pup Weddell seals at rest in air. \circ = rates taken by electrocardiograph.

Metabolic Rates

Seven tests of from 15 minutes to one hour duration on a pup Weddell seal showed rather consistent results (Table II). Oxygen consumption averaged $35.3 \text{ cc/min/k}^{3/4}$ and carbon dioxide production was $25.5 \text{ cc/min/k}^{3/4}$. The respiratory quotient (R.Q.) was 0.727. High metabolic rates for seals have previously been shown by Scholander (1940), Scholander, *et al.* (1950), Irving and Hart (1957) and Davydov and Makarova (1964). Very few mammals show such exception to the Benedict "mouse to

elephant curve" (Brody, 1945, p. 370; Kleiber, 1961, p. 201). Though we do not compare our tests with those of others, because a pup was used and some elevation of rate is to be expected, we do wish to note the extremely high metabolic rate found here.

Thermal Gradients in the Superficial Tissues

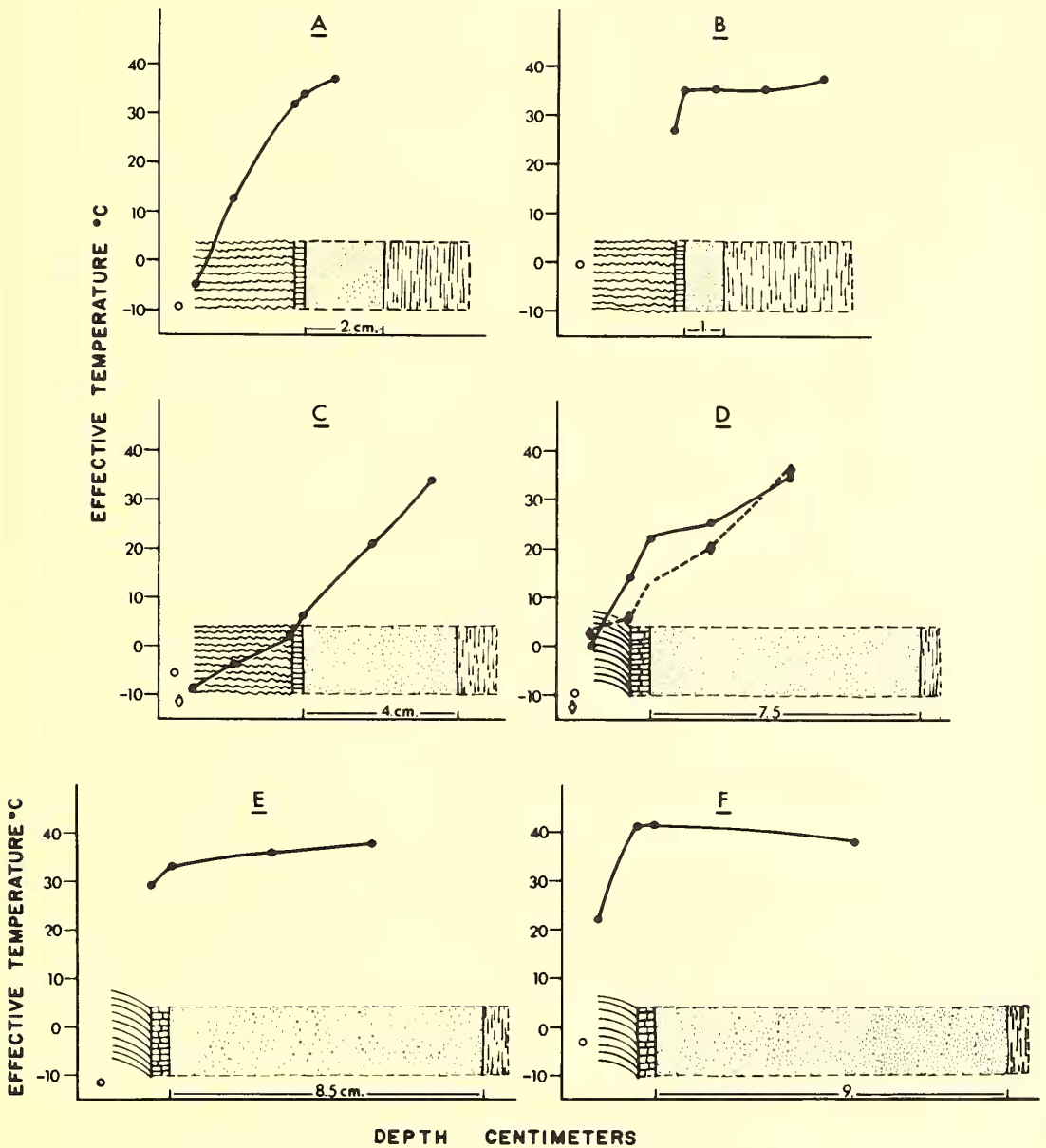
Temperature gradients were recorded through the fur, skin, and subcutaneous tissues of living pups and of adults immediately after they were killed (Text-fig. 7). In young pups without much

TABLE II
METABOLIC RATES OF A PUP WEDDELL SEAL

Chamber Temperature	O ₂ cc/min/k ^{3/4}	CO ₂ cc/min/k ^{3/4}	R.Q. CO ₂ /O ₂	Duration of Test, Minutes
3 to 6	40.9	28.7	0.702	15
5 to 8	16.9	12.5	0.740	15
-3 to 0	26.5	18.8	0.709	15
-2 to 4	43.8	30.7	0.706	60
0 to 1	42.25	30.75	0.727	30
-1 to 3	39.8	30.5	0.766	30
-1 to 3	36.5	27.0	0.740	15
Averages	35.3	25.5	0.727	

blubber (7A & B), skin surfaces were 32 and 27°C at effective temperatures of -8 and 0°C. Gradients were taken up mostly in the thick lanugo coat. In contrast, a fat pup (7C), well toward weaning and damp at the time of recording, had a low skin temperature, illustrating the

effect of dampness in inducing vasoconstriction. Three examples of adults illustrate three contrasting gradients. The first (7D) contrasts temperatures from the shaded side with that of the sunny side of the seal. The gradient was not so steep in shade as under direct insolation. Con-



TEXT-FIG. 7. Temperature gradients through the superficial tissues of pup and adult Weddell seals immediately after death. Skin and blubber thicknesses at the site of measurement are indicated beneath each section. Air temperatures within 1 meter of the animal are indicated by the open circle to the left of each section. Lanugo = ~~~~. Adult hair = ~~~~. Skin = [||||]. Blubber = [:::]. Muscle = [||||]. On section D, diamonds connected by a dotted line indicate a gradient through the tissues on the shaded side of the seal.

trasting was an example of elevation of skin temperature to plateau levels (7E) in which the gradient is mostly in the fur. The last (7F) shows the effect of intense insolation in which the skin was over 40°C and deeper tissues 38°C, indicating that heat gained at the surface was distributed to other parts of the body through the circulatory system. Ray and Fay (1968) show a similar situation in the walrus in which high surface temperatures are induced by insolation.

Effect of Insolation on Fur and Skin

The lanugo of the Weddell seal is silver-tan to gray in color, darkest on the back (Plate I). Flat wavy hairs form a thick coat about 2.0-2.5 cm thick. Short hairs of the juvenile coat are present under the lanugo from birth and grow to replace the lanugo at about four to six weeks of age. The juvenile and adult coats are medium to dark gray, darkest on the back, flecked with black and white irregular blotches and spots, especially below. The primary hairs are flattened and about 1 cm in length, pointing backward, but tending to curve forward when dry. There are fine secondary hairs about 0.5 cm in length. Scheffer (1964) gives the density of primary hairs, on formalin-preserved skin, as 34/cm² with a maximum length of 1.3 cm, and the number of secondary hairs per unit as three to five.

Five tests were made of the effect of insolation on tanned skins of pup and adult seals. Skins were spread half in shade and half under strong sun. Ambient shade and black-bulb temperatures under sun were taken adjacent to the skins. The results of the tests were almost identical and examples of adult and pup will be considered (Text-fig. 8 A & B). Air temperature in shade did not change throughout the tests. Skin and fur-surface temperatures in shade rose somewhat higher than air temperatures in shade for both adult and pup, probably owing to radiation reflected from a nearby white building. Black-bulb temperatures in sun rose rapidly, but fur-surface and skin temperatures of adult and pup rose faster and to a higher level. Cloudiness occurred about two-thirds through the tests and produced a fall in black-bulb temperatures with a corresponding fall in skin and fur temperatures.

Several explanations are possible for the rapid and extensive rise in skin and fur temperature under sun. The simplest is analogous to that of Krog (1955) for pussy willow catkins. The shiny, translucent hairs allow sunlight through to the skin, where heat is absorbed, but they do not allow as much heat radiation to escape. The result is the familiar "green house" effect.

A second phenomenon, a lenticular effect of the flattened hairs in concentrating the sun's rad-

iation, may also be in evidence as suggested by Fay (pers. comm.). Adult hairs are flatter and more regularly arranged than pup lanugo, and we see that adult skin temperature rises faster and higher than that of the pup. However, in the increasing cloudiness indicated, the adult skin temperature fell, whereas the thick lanugo trapped warm air so that no similar fall in the pup skin temperature was observed.

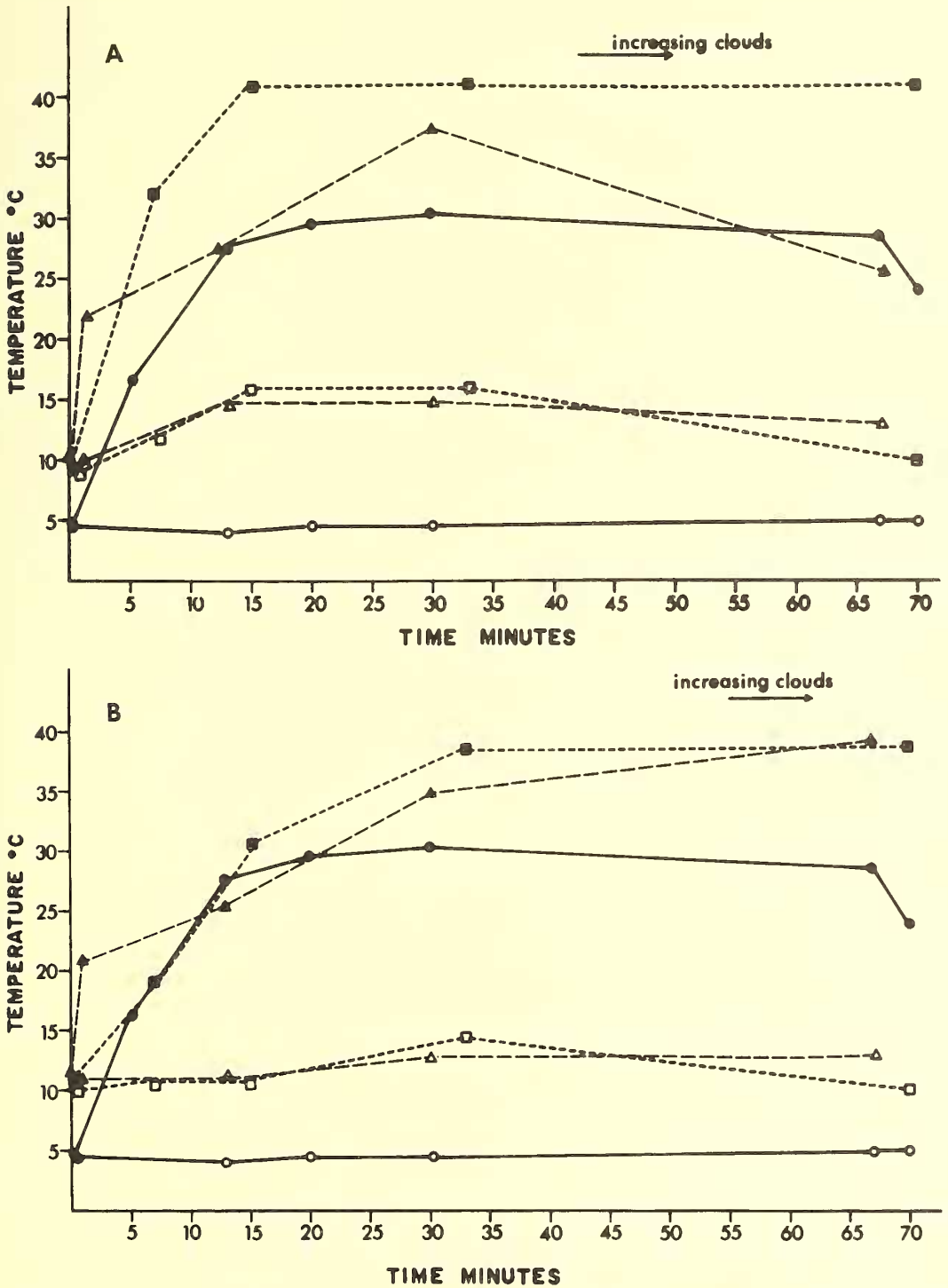
The Role of Behavior

The Weddell seal does not exhibit the array of thermoregulatory behavior displayed by walruses (Fay & Ray, 1968). Nevertheless, some behavioral patterns are marked. The most notable of these is the predilection of the Weddell seal for sun. On hot, dry days Weddell seals were observed basking on the surface in numbers not seen in the same localities during inclement weather. During sunny weather, the seals, especially pups, moved about on the ice; it appeared to us that flippers were spread more than during cloudy weather and that the seals sought the sun's ray by orienting with their long axis perpendicularly to them. To test the latter point, seals were counted, principally from the air, and their orientation to the sun recorded photographically (Table III). During cloudy weather about half the seals were oriented perpendicularly to the sun, but during sunny weather about four-fifths were oriented in this way. Plate II shows two examples of aerial photographs from which data were taken.

During inclement or very cold weather, Weddell seals are notably either sluggish in air or retreat to water (Smith, 1965). However, escape to water is usually not possible for mothers and their pups. At these times, pups remain in the lee of their mothers, moving out of the lee and resuming activity only when effective temperatures reach about -20°C. We have some evidence that mothers induce activity on the part of the pups and/or that nursing keeps the pups somewhat active even in the harshest weather. This probably serves to prevent drifting in and allows crystals of frozen moisture to fall off, thus keeping the lanugo fluffy and dry. Plate I shows a pup and its mother just after a severe blizzard. The pup has resumed activity and is thus dry and warm and free of snow.

DISCUSSION

Scholander (1955), in reviewing the climatic adaptations of homeotherms, has reasoned that clues to thermoregulation are principally to be found in the control of heat dissipation. He has further stated that basal metabolic rate and internal temperature are not adapted to climate and that physical insulation and adaptation of



TEXT-FIG. 8. The effect of insolation on the fur and skin surfaces of tanned, dry adult (A) and pup (B) Weddell seal skins. Air temperature in shade (---○---). Black bulb temperature in sun (---●---). Fur surface temperature in shade (---△---). Fur surface in sun (---▲---). Skin surface in shade (---□---). Skin surface in sun (---■---).

TABLE III
ORIENTATION OF WEDDELL SEALS TO SUN

Sky	Total Seals	Percentage of Total Perpendicular to Sun
Clear-sunny	63	65
	28	78
	40	70
	68	76
	33	79
	16	71
	32	66
	60	92
	4	100
	13	77
	24	100
	16	88
	19	79
	14	86
	12	92
	28	64
	28	68
	24	79
	64	83
	40	63
	41	73
	26	85
	62	84
	31	81
	44	89
	Average percentage	79.5
Cloudy or partly cloudy	38	50
	100	60
	64	70
	68	53
	40	45
	33	58
	46	39
	34	56
	82	49
	76	47
	49	53
	35	51
	41	56
	90	52
		Average percentage

critical temperatures are the major mechanisms for heat dissipation control. These observations strongly imply that skin temperature should vary directly with ambient temperature in order exactly to balance metabolic heat production with heat dissipation. Irving and Hart (1957) and Hart and Irving (1959) show such regressions for restrained seals in experimental conditions.

Fay and Ray (1968) and Ray and Fay (1968) have found that for wild and unrestrained walrus, a plateau of skin temperatures rather than a straight regression is the case and

that behavior is at least as important as physical or physiological mechanisms in thermoregulation. Further, tolerance limits, rather than critical physiological limits, were indicated to be significant in an animal that, by behavioral means, is probably able to maintain thermoneutrality beyond the limits indicated by physiology alone. The present study on the Weddell seal confirms the observations made for the walrus. Our results indicate, following the suggestion of Brody (1945, p. 295), that although critical values are theoretically interesting, they probably have little significance under natural conditions.

The Weddell seal is a very large species, probably the heaviest except the elephant seal, *Mirounga sp.*, and the longest except the elephant seal and the leopard seal, *Hydrurga leptonyx*. The lanugo of pups is thick, as described above. The blubber appears to be the thickest of any seal except the elephant seal. At birth the nose-tail length is about 125 cm and the belly blubber measures about 1 cm. The blubber is about 5 to 6 cm at weaning, when the pup has grown to about 160 cm. Yearlings are 160 to 180 cm long and have about 4 cm of blubber in November. Females are inclined to be a little longer than males. Large ones are about 300 cm, and the blubber is 6 to 9 cm thick. Blubber is not of constant thickness the year around but varies with nutrition, nursing, and molting. Hart and Fisher (1964) have given thickness of blubber for several species, and the thickest given is that of the Arctic harp seal, at 6.3 cm. Since the tropical Hawaiian monk seal's blubber is 4.5 cm, the thickness of blubber is probably of little significance under conditions of vasodilation when blubber is bypassed by blood flowing to the surface. But blubber thickness is of significance under conditions of vasoconstriction. Therefore, a thick blubber becomes vitally important to polar species only when such a species is swimming in ice water or exposed to harsh conditions in air.

We have presented data that clearly show that the wild, unrestrained Weddell seal, like the walrus (Ray & Fay, 1968), vasodilates in air and that the dry skin temperature reaches a high "plateau" level of about 34°C. This high plateau is reached, however, only on that part of the seal not in contact with the snow or ice substrate, against which the skin is vasoconstricted. Heat gained on one surface of the seal is probably distributed through the body by the circulatory system. We have also shown that the Weddell seal actively seeks the warmth of insolation by orienting with the long axis of the body perpendicularly to the sun's rays.

As shown by the time-temperature curves of Text-fig. 8, Weddell seals are aided in the gaining of heat by what is familiarly termed the "greenhouse effect," wherein heat gained by the sun's radiation is conserved by an overlying layer of hair. This is a new observation for pinnipeds. It is primarily an adaptation in which Weddell seals are able facultatively to take advantage of insolation, when the latter is sufficiently strong, in an environment that is the coldest known for mammals. The saving of metabolic heat due to this efficient utilization of insolation is presumably considerable.

Pups in lanugo appear to be better adapted to temperatures well below freezing than to temperatures close to or above 0°C. Wet hair has little insulating value. At low temperatures, dampness from birth, melting ice, urine, or excrement freezes and falls off so that the lanugo remains fluffy and dry. Observations of late-born Weddell seals exposed to high temperatures and dampness tend to confirm this observation. For example, a seal estimated at about a week's age and still quite thin was observed during a warm, wet snow fall on November 7. After a few similar warm, wet days, this seal was found near its mother, still thin. After nine days it died. We speculate that the cause of death was chill accompanying dampness and near 0°C weather of the period. We have subsequently observed that early born pups gain weight faster than pups in warmer, wetter conditions. The function of the lanugo is to retain body heat and to prevent undue heat loss from skin, which must remain at relatively high plateau temperatures to grow (Feltz & Fay, 1967), and this is most effectively performed when the lanugo is dry and an effective insulator, even in very cold weather.

Insights into the critical limits of the Weddell seal were obtained while transporting them from Antarctica to the New York Aquarium and also during their gradual acclimatization to temperate climate there. In November 1963, six Weddell seals were flown from Antarctica to New York in about two days. Temperatures in the aircraft ranged from 12 to 28°C, the latter during a stopover in American Samoa, where air-conditioning facilities were limited. There, after an hour at 24 to 28°C, an adult male and female became hyperactive, even showing signs of delirium, tossing and rolling in their crates. Flipper temperatures were as high as 39°C and body skin as high as 37°C. Their breathing rates were 16 per minute, higher than any rates taken in the field. Both animals died within 12 hours of this exposure. Two pups showed similar stress, one biting its flippers and the other showing

greatly increased activity when air temperatures reached only 18°C. One of the pups also died shortly after leaving Samoa. Two remaining seals, a juvenile male and an adult female, remained calm and lived. The juvenile male astonished us by copiously taking water from a paper cup held for it. Thus, the upper critical temperature limit, suddenly imposed on Antarctic-acclimatized animals, is probably not reached at temperatures under 20°C.

The above mentioned female, juvenile, and pup and two additional Weddell seals brought from Antarctica in February 1965 underwent gradual acclimatization during the New York winter and spring. None of these showed ill effects from effective temperatures as high as 32 to 34°C, often lying out and basking, their skins fully dry, under the heat of the summer sun. They did not even choose to escape to the 12°C water constantly available to them. Similar acclimatization is indicated for walrus by Ray and Fay (1968), but the Weddell seal apparently acclimatizes to even higher temperatures than the walrus, as indicated by the lack of escape behavior. It is, therefore, probable that upper critical limits of acclimation and acclimatization (see Hart, 1957, for further definition) are not realistic parameters to be used for the Weddell seal in its natural environment.

We could not observe seals at their probable lower critical temperatures in the field and had no means to expose Weddell seals to extremely low temperatures in captivity. Wild seals were observed to escape from severe weather conditions lower than effective temperatures of -30°C by entering the water, and the number of seals on the surface appears to be directly proportional to effective temperature (Smith, 1965, 1966). However, judging from experimental work on the harp seal, *Phoca groenlandica*, (Irving & Hart, 1957), we would not expect the lower critical temperature to be above -40°C. A similarly low critical temperature is indicated here by virtue of the high skin temperatures found at effective temperatures of -20°C and below.

Thus thermoregulation of polar amphibious mammals, as pinnipeds, presents two different situations: that in air, where we believe vasodilation and high skin temperatures are normal, and that in water, where vasoconstriction and low skin temperatures are normal. In both, we think the animal seeks to maintain thermoneutrality. By behavioral means such as orientation to sun in good weather or escape to water or retreat to the lee of the wind in inclement weather, the Weddell seal, as the walrus, seeks to avoid critical limits and to delimit its tolerance zone. The

upper and lower in-air critical limits are not realistic parameters for assessment of natural adaptation but only indicate one of the many imposed limits that may be superseded by behavior, as in the case of walrus brooding (Ray & Fay, 1968). We conclude that upper critical temperatures are rarely if ever reached in the natural environment of polar pinnipeds. Lower critical temperatures are limited indications of adaptation because both the walrus and the Weddell seal rarely expose themselves to such low temperatures but choose to escape to water and maintain thermoneutrality there well before lower limiting in-air temperatures are reached.

The primary differences between the walrus and the Weddell seal appear to be found in the tolerance zone, its relationship to distribution of the species, and the behavior exhibited within it. The walrus, especially the calf, is much more sensitive to cold than the pup or adult Weddell seal. Both species show some escape to water in inclement weather of -20 to -30°C effective temperature, but the walrus probably does so nearer its lower critical limit than the Weddell seal. The lower critical temperature for walrus calves is about 5°C and the lower limit of tolerance is extended by brooding to a lower temperature. The Weddell pup tolerates at least -30°C . However, we wish to point out that much more work is needed on unrestrained pinnipeds at their lower tolerance limit. Data are better for higher temperatures, and the walrus probably is limited in its distribution by its upper tolerance temperature of about 18°C and the habit of persistent huddling. The Weddell seal cannot be so limited. It is able to withstand, and shows no escape from, climate not remotely possible in the Antarctic environment. In both, acclimatization is possible, but, again, in the Weddell seal to a higher temperature. Finally, the walrus exhibits an array of behavior that serves to extend the tolerance zone near to or beyond probable critical physiological limits whereas in the Weddell seal few traits of behavioral thermoregulation are shown. This difference might to an extent be due to the presence of a coat of insulating hair in the pup and adult Weddell seal, contrasted with the practically bare-skinned walrus.

SUMMARY AND CONCLUSIONS

1. Parameters of physiological function and behavior were measured in unrestrained Weddell seals in an effort to delimit the tolerance zone and its possible relationship to distribution. Surface temperatures were obtained on the fur, body skin, and rear flippers. Heart, breathing, and metabolic rates were obtained. Tanned skins

were placed under shade and in sun in order to measure fur- and skin-temperature changes with time. Our measure of ambient temperature is "effective temperature," which includes the effects of wind and insolation.

2. Few measurements were made of rectal temperature, but about 37°C appears to be normal.

3. Skin temperatures during immersion appear to be only slightly higher than water temperature. After the seals' emersion into air, skin temperatures rise rapidly, faster in warmer air.

4. Dry skin and flipper temperatures did not rise as straight regressions with air temperature, but leveled off at about 34°C at effective temperatures above -13 to -15°C for adults and pups. Pups had skin temperatures in excess of 30°C at effective temperature of over -21°C . Fur surface temperatures, however, did rise directly with effective temperatures.

5. There was little or no correlation between effective temperature and breathing and heart rates of adults or pups, except possibly for the heart rate of the pup, which may have been minimal at about -5° . Pups had extremely high metabolic rates, in excess of any seal yet tested.

6. Gradients through the skin and blubber show that most of the gradient is taken up in the lanugo of the dry pup and in the fur, skin, and blubber of the adult or wet pup. The blubber of the adult Weddell seal is thicker than that of any other phocid except the elephant seal.

7. Tanned skins under sun show a marked "greenhouse effect" in which both fur and skin temperatures rise faster and higher than black-bulb temperatures. A possible lenticular effect of the flattened translucent hairs of the adult is indicated in which the adult skin is warmed faster than that of the pup, but also cools faster in shade.

8. Behavioral thermoregulation is not as marked in the Weddell seal as in the walrus. Seals show orientation to sun and seek lee from winds and storms. They also show escape to water from harsh weather conditions.

9. The upper critical limit of the nonclimatized Weddell seal in air is in excess of 20°C and the lower limit in air is probably at least as low as -40°C . The upper limit is not a realistic parameter of in-air adaptation or of distribution. The lower limit is probably at least -40°C and is not often experienced by most seals because before that limit is reached they probably escape to water. The seal, like the walrus, probably maintains thermoneutrality when at rest in either air or water.

10. The principal difference between the pup and the adult Weddell seal lies in the lanugo hair of the latter. Its function has been found, as expected, to provide an insulative coat in which the thermal gradient may be taken up before sufficient blubber is present for that purpose. The lanugo is most effective when thoroughly dry and so the pup Weddell seal is best protected at low effective temperatures when moisture will freeze and not wet fur or skin.

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LITERATURE CITED

- BERTRAM, G. C. L.
1940. The biology of the Weddell and Crabeater seals, with a study of the comparative behaviour of the Pinnipedia. Brit. Mus. (Nat. Hist.) Sci. Repts. Brit. Graham Land Exped. 1934-1937, 1:1-139.
- BRODY, S.
1964. Bioenergetics and growth. Hafner Publishing Co., New York.
- DAVYDOV, A. F. AND A. R. MAKAROVA
1964. Changes in heat regulation and circulation in newborn seals on transition to aquatic form of life. Fiziol. Zhur. SSSR, 50(7): 894. (Transl. Suppl., Fed. Proc., 24(4): T563-T566.)
- EAGAN, C. J.
1964. Effect of air movement on atmospheric cooling power. Excerpted from "A review of research on military problems in cold regions." AAL-TDR-64-28, Arctic Aero-medical Laboratory, Ft. Wainwright, Alaska, November 1964, 1-160.
- FAY, F. H., AND CARLETON RAY
1968. The influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. Zoologica, 53(1) 1-18.
- FOLK, G. E.
1966. Introduction to environmental physiology: environmental extremes and mammalian survival. Lea & Febiger, Philadelphia. 308 pp.
- HART, J. S., AND H. D. FISHER
1964. The question of adaptations to polar environments in marine mammals. Fed. Proc., 23(6):1207-1214.
- HART, J. S., AND L. IRVING
1959. The energetics of harbor seals in air and in water with special consideration of seasonal changes. Can. Jour. Zool., 37:447-457.
- IRVING, L., AND J. S. HART
1957. The metabolism and insulation of seals as bare-skinned animals in cold water. Can. Jour. Zool., 35:497-511.
- KING, J. E.
1964. Seals of the world. Brit. Mus. (Nat. Hist.), London.
- KLEIBER, M.
1961. The fire of life. John Wiley & Sons, Inc., New York. 454 pp. *

- KOOSMAN, G.
1965. Maximum diving capacities of the Weddell seal, *Leptonychotes weddelli*. Science, 151(3717):1553-1554.
- KROG, J.
1955. Notes on temperature measurements indicative of special organization in arctic and subarctic plants for utilization of radiated heat from the sun. Physiologica Plantarum, 8:836-839.
- LINDSEY, A. A.
1937. The Weddell seal in the Bay of Whales, Antarctica. Jour. Mammalogy, 18(2): 127-144.
- LITTLEPAGE, J. L.
1963. Diving behavior of a Weddell seal wintering in McMurdo Sound, Antarctica. Ecol., 44(4):775-777.
- MANSFIELD, A. W.
1958. The breeding behaviour and reproductive cycle of the Weddell seal (*Leptonychotes weddelli* Lesson). Sci. Repts., Falkland Isl. Dep. Sur. No. 18.
- RAY, CARLETON
1965. Physiological ecology of marine mammals. Bioscience, 15(4):274-277.
1966. The ecology of Antarctic seals. Antarctic Journal, July-August, 1(4):143-144.
1967. Social behavior and acoustics of the Weddell seal. Acoustics Journal, 2(4): 105-106.
- RAY, CARLETON, AND F. H. FAY
1968. The influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). II. Evidence from physiological characteristics. Zoologica, 53(1):19-32.
- RAY, CARLETON, AND D. O. LAVALLEE
1964. Self-contained diving operations in McMurdo Sound, Antarctica: observations of the sub-ice environment of the Weddell Seal, *Leptonychotes weddelli* (Lesson). Zoologica, 49(3):121-136.
- SAPIN-JALOUSTRE, J.
1952. Les phoques de Terre Adelie. Mammalia, 16:179-212.
- SCHEFFER, V. E.
1958. Seals, seal lions and walruses. Stanford University Press, Stanford, Calif.
1964. Hair patterns in seals (Pinnipedia). Jour. Morph., 115(2):291-301.
- SCHEVILL, W. E., AND W. A. WATKINS
1965. Underwater calls of *Leptonychotes* (Weddell seal). Zoologica, 50(1):45-46.
- SCHOLANDER, P. F.
1940. Experimental investigations on the respiratory function in diving mammals and birds. Hval. Skrift., No. 22.
1947. Analyzer for accurate estimation of respiratory gases in one-half cubic centimeter samples. Jour. Biol. Chem., 169:235-250.
1955. Evolution of climatic adaptation in homeotherms. Evol., 9(1):15-26.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, AND L. IRVING
1950. Adaptation to cold in Arctic and tropical mammals and birds in relation to temperature, insulation, and basal metabolic rate. Biol. Bull., 99(2):259-271.
- SMITH, M. S. R.
1965. Movements of the Weddell seal in McMurdo Sound, Antarctica. Jour. Wild. Man., 29(3):446-447.
1966. Studies on the Weddell seal in McMurdo Sound, Antarctica. Ph. D. Thesis, unpublished, University of Canterbury, Christchurch, N.Z.
- WILSON, E. A.
1907. Mammalia (whales and seals). Nat. Ant. Exped., 1901-1904. Natural History, 2: 1-66.

EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Female and nursing pup Weddell seals, illustrating the color pattern and the texture of the fur.
- FIG. 2. Penned female and pup Weddell seals just after a severe storm. The female is still covered with snow and has not yet resumed full activity. The pup has resumed

activity with the result that the snow has fallen off, leaving the lanugo fluffy and dry.

PLATE II

- FIG. 3. Weddell seals at random orientation on a cloudy day.
- FIG. 4. Weddell seals oriented perpendicularly to the sun on a clear, sunny day.